Experience-dependent Modulation of Category-related Cortical Activity

Linda L. Chao[1,2], Jill Weisberg[1] and Alex Martin[1]

[1]Laboratory of Brain and Cognition, National Institute of Mental Health, Bethesda, MD and [2]VA Medical Center, 4150 Clement Street, 114Q, San Francisco, CA, USA

Naming pictures of objects from different categories (e.g. animals or tools) evokes maximal responses in different brain regions. However, these 'category-specific' regions typically respond to other object categories as well. Here we used stimulus familiarity to further investigate category representation. Naming pictures of animals and tools elicited category-related activity in a number of previously identified regions. This activity was reduced for familiar relative to novel stimuli. Reduced activation occurred in all object-responsive areas in the ventral occipito-temporal cortex, regardless of which category initially produced the maximal response. This suggests that object representations in the ventral occipito-temporal cortex are not limited to a discrete area, but rather are widespread and overlapping. In other regions (e.g. the lateral temporal and left premotor cortices), experience-dependent reductions were category specific. Together, these findings suggest that category-related activations reflect the retrieval of information about category-specific features and attributes.

Introduction

A number of investigators have identified distinct cortical regions that respond differentially to various object categories (Kanwisher *et al.*, 1997; Aguirre *et al.*, 1998; Chao *et al.*, 1999a). In a typical experiment on category-related brain activity objects from different categories are presented. If one brain region responds maximally to one type of object (e.g. human faces) relative to others, it is taken as evidence in favor of category specificity. However, the 'category-specific' regions are rarely silent to other object categories, but rather show a smaller yet significant response. For example, in an object-naming study it was reported that, while the maximal response in the lateral aspect of the fusiform gyrus was associated with naming pictures of animals and in the more medial aspect with naming tools, the 'non-preferred' category elicited smaller yet significant responses in each of these regions relative to a scrambled object baseline condition (Chao *et al.*, 1999a).

In one view the smaller response to other object categories may simply represent a non-specific response to any category of objects. Alternatively, this reduced response may reflect neural activity that is part of the specific representation of the other categories (Haxby *et al.*, 2000; Martin *et al.*, 2000; Martin and Chao, 2001). Within this view, the representation of an object category is not restricted to a single anatomically discrete area (i.e. the region of maximal response) but rather is more widespread. This widespread representation is reflected in functional magnetic resonance imaging (fMRI) data as overlapping regions of activity that may have multiple peaks and valleys.

In the present study we used object familiarity for distinguishing between these alternatives. Many investigators have observed that object repetition reduces the magnitude of the associated fMRI signal (Martin *et al.*, 1995a; Buckner *et al.*, 1998; Tootell *et al.*, 1998; Grill-Spector *et al.*, 1999; Van Turennout *et al.*, 2000). While the neuronal mechanism underlying this repetition suppression effect has not been fully delineated, one suggestion is that it reflects the creation of sparser yet more object-specific representations that facilitate object recognition (Desimone, 1996; Wiggs and Martin, 1998) [however a different account can be found elsewhere (James *et al.*, 1999)]. Regardless of the underlying mechanism, prior experience with an object would be expected to reduce the magnitude of the fMRI response associated with that object. If representations of object categories are, in part, widespread and overlapping, then repetition should reduce both the response to the maximally activating category as well as the smaller response associated with the other object category. However, if the smaller peak is merely a non-specific response then repetition should only modulate the maximal but not the smaller response.

Although the type of information represented by category-related activations remains to be determined, it has been proposed that they represent the retrieval of stored information about specific object features and attributes (Martin *et al.*, 2000). For example, differential activity has been reported in the posterior ventral temporal cortex for human faces, four-legged animals, tools, houses/buildings, letter strings and chairs (Puce *et al.*, 1996; Kanwisher *et al.*, 1997; McCarthy *et al.*, 1997; Aguirre *et al.*, 1998; Epstein and Kanwisher, 1998; Chao *et al.*, 1999a,b; Haxby *et al.*, 1999; Ishai *et al.*, 1999). As these activations are located within the ventral object-processing stream, they may reflect the retrieval of information about object form. Activity for human faces (Kanwisher *et al.*, 1997; Chao *et al.*, 1999a; Haxby *et al.*, 1999) and animals (Chao *et al.*, 1999a,b) has been found in the posterior region of the superior temporal sulcus (STS) and in the left middle temporal gyrus for naming and identifying tools (Martin *et al.*, 1996; Mummery *et al.*, 1996; Cappa *et al.*, 1998; Chao *et al.*, 1999a; Moore and Price, 1999). These lateral temporal regions lie just anterior to motion perception area MT/V5 (Zeki *et al.*, 1991). Moreover, previous studies have demonstrated that the STS responds to the perception of biological motion (Oram and Perrett, 1994; Bonda *et al.*, 1996; Puce *et al.*, 1998) [a review can be found elsewhere (Allison *et al.*, 2000)] and the left middle temporal gyrus is active when subjects generate action words (Wise *et al.*, 1991; Martin *et al.*, 1995b; Fiez *et al.*, 1996). Thus, it has been proposed that the face- and animal-related responses in the STS may represent the activation of stored information about biological motion that is needed for identifying these objects as distinct entities, while the tool-related response in the left middle temporal gyrus may represent stored information about motion that is associated with manmade, manipulable objects. Finally, tool-related responses that have been found in the left premotor and left posterior parietal cortices (Chao and Martin, 2000) may represent stored information about object use-associated motor patterns, as these areas have previously been

implicated in motor imagery and control (Decety *et al.*, 1994; Stephan *et al.*, 1995; Grafton *et al.*, 1996; Binkofski *et al.*, 1998).

If category-related activity represents the activation of stored information about the features necessary for distinguishing objects as distinct entities, then experience should only modulate responses to object categories that are associated with the represented feature. For example, if category-related activity in the left premotor cortex represents activation of stored information about object use-associated motor patterns, then prior exposure should only modulate responses to naming tool but not animal pictures in that region. In the present study, subjects gained experience with a subset of animal and tool pictures by performing naming and other tasks with them. Four days later they were scanned while naming these and novel pictures of animals and tools in order to evaluate the effect of experience on the pattern and magnitude of the category-related cortical activity.

Materials and Methods

Subjects
Seven subjects (two men and five women of age range 22–32 years) participated in the imaging experiment and 12 subjects (three men and nine women of age range 21–37 years) participated in the behavioral experiment. All subjects gave written informed consent in accordance with the procedures and protocols approved by the National Institute of Mental Health Institutional Review Board.

Stimuli and Design
The stimuli consisted of 720 gray-scale photographs of animals and tools and phase-scrambled images of these stimuli. Four days prior to the experiment the subjects were familiarized with 360 photographs (six exemplars of 30 different animals and 30 different tools) outside of the scanner by performing naming, one-back and delayed match-to-sample tasks. By the end of the training session the subjects had seen each of the 360 photographs of the animals and tools four times. Four days later the subjects returned in order to perform a naming task (stimulus duration = 1.5 s and interstimulus interval = 0.5 s) with 720 gray-scale photographs of animals and tools (six exemplars of 60 different animals and 60 different tools). Half of the stimuli were old pictures from the training session and half were new pictures. The stimuli were counterbalanced across the subjects and presented in a pseudo-randomized blocked design. Separate blocks of photographs of new animals, new tools, old animals and old tools were alternated with blocks of phase-scrambled images. There was a total of six runs. Each run consisted of 16 blocks with 15 items each and lasted 5 min and 20 s. The subjects in the fMRI study performed the naming task silently and the subjects in the behavioral study named the pictures aloud outside the scanner while their accuracy and voice onset times were recorded.

Imaging Parameters
Anatomical and functional data were acquired on a 1.5 T scanner (General Electric, Milwaukee, WI). Structural data were acquired using a fast SPGR sequence (124 sagittal slices of 1.5 mm thickness). Functional data were acquired using a gradient-echo, echo planar imaging sequence (T_R = 3 s, T_E = 40 ms, flip angle = 90°, 22 contiguous 5 mm slices, 3.75 × 3.75 × 5 mm in-plane resolution and 108 images per slice).

Image Analysis
Functional images were registered using AIR v. 3.08 (Woods *et al.*, 1998) before a 1.2 voxel smoothing filter was applied to each scan. Multiple regression was performed on each voxel's time-series using AFNI v. 2.21 (Cox, 1996). Three regressors of interest were used. The first regressor revealed differences between meaningful objects and phase-scrambled images. The second and third regressors revealed differences between naming photographs of animals and tools and naming old and new photographs respectively. Individual Z-maps were squared, normalized to standardized space (Talairach and Tournoux, 1988) and added to create a group χ^2-map.

Region of interest masks were drawn on the group-averaged activation maps and applied to each individual's data in order to extract MR time-series and the center of mass for each region. A two-stage process was used for extracting the time-series. First, the regions were restricted to voxels that exceeded a threshold of $Z > 3.09$ ($P < 0.001$ per voxel) for the objects versus phase-scrambled images regressor. Voxels surviving this test were interrogated by the second and third regressors of interest with a threshold at $Z > 1.96$ ($P < 0.05$ per voxel). The time-series were converted to percent change scores and submitted to a multiple regression analysis in order to measure the size of the effect for each stimulus type (new and old animals and new and old tools). The resulting beta weights for all subjects were then submitted to a repeated-measures analysis of variance, treating subjects as a random factor, in order to test for the main effects of category and experience and the interaction between category and experience.

Results

Behavioral Data
The naming latencies from the subjects who participated in the behavioral experiment documented a significant long-term learning effect. The subjects were faster to name pictures of animals and tools that they had seen 4 days earlier during the study phase (mean reaction time ± SD for old pictures = 890 ± 57 ms) than they were to name new pictures (mean reaction time ± SD = 939 ± 61 ms) [priming effect $F(1,11) = 47.2$ and $P < 0.0001$]. There were no significant differences between the priming effects for the pictures of animals and tools (interaction between stimulus type and experience $F = 2.8$ and $P > 0.1$).

fMRI Data
The comparison of silently naming animals versus silently naming tools revealed category-related activity in several cortical regions. Consistent with previous results (Chao *et al.*, 1999a), naming animal pictures elicited a larger bilateral response than naming tools in the calcarine cortex, middle occipital gyrus and the lateral aspect of the fusiform gyrus, whereas naming tool pictures elicited a larger response than naming animals bilaterally in the medial aspect of the fusiform gyrus (see Table 1 and Fig. 1). Naming pictures of animals and tools that were

Table 1

Regions that show differential responses to naming pictures of animals and tools

Region	Selectivity	Learning effect (N > 0)	Interaction (category × experience)	Talairach coordinates (x,y,z)		
Occipital lobe						
L calcarine sulcus	A > T ***	*	NS	−13	−88	4
R calcarine sulcus	A > T **	**	NS	19	−87	5
L middle occipital gyrus	A > T *	**	NS	−37	−74	2
R middle occipital gyrus	A > T **	**	NS	39	−73	3
Ventral temporal lobe						
L lateral fusiform gyrus	A > T **	**	NS	−38	−58	−10
R lateral fusiform gyrus	A > T ***	***	NS	36	−57	−10
L medial fusiform gyrus	T > A **	**	NS	−25	−57	−7
R medial fusiform gyrus	T > A **	***	NS	22	−54	−5
Lateral temporal lobe						
R superior temporal sulcus	A > T ***	**	*	43	−40	19
L middle temporal gyrus	T > A ***	*	*	−44	−55	2
Parietal lobe						
L inferior parietal sulcus	T > A ***	*	*	−31	−47	44
Frontal lobe						
L premotor cortex	T > A **	**	*	−44	7	32

Center-of-mass coordinates from group-averaged statistical maps ($n = 7$) are reported in normalized stereotaxic space (Talairach and Tournoux, 1988). Z-scores > 4.50 for all regions.

R, right; L, left; A, animal; T, tool; O, old; N, new.

Significance levels based on random effects ANOVA of the time-series data: *$P ≤ 0.05$; **$P ≤ 0.01$; ***$P ≤ 0.001$.
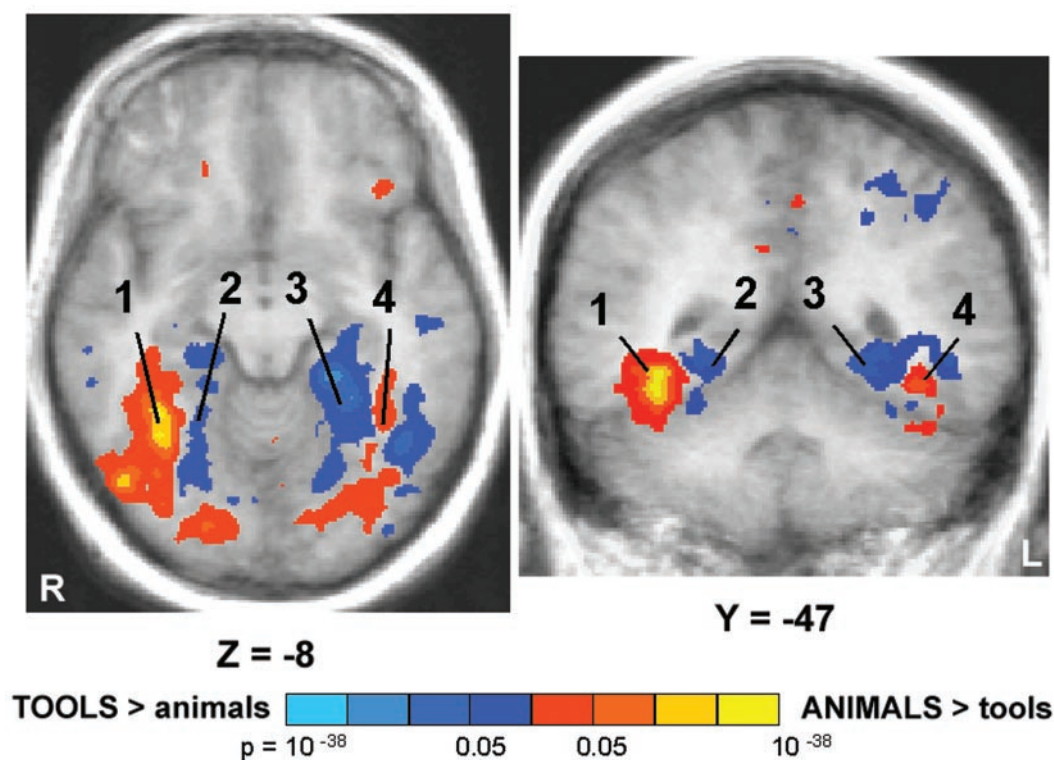
Figure 1. fMRI response in the ventral occipito-temporal cortex during animal and tool naming. The averaged significance maps from seven subjects are overlaid on an averaged anatomical image from the same subjects. The maps, which are illustrated in axial (z = –8) and coronal (y = –47) sections, show the locations of four ventral occipito-temporal regions (1, right lateral fusiform; 2, right medial fusiform; 3, left medial fusiform; 4, left lateral fusiform) that responded differentially to naming pictures of animals and tools. Regions that responded maximally to naming animals are shown in the red–yellow color spectrum and regions that responded maximally to naming tools are shown in the blue–violet color spectrum.
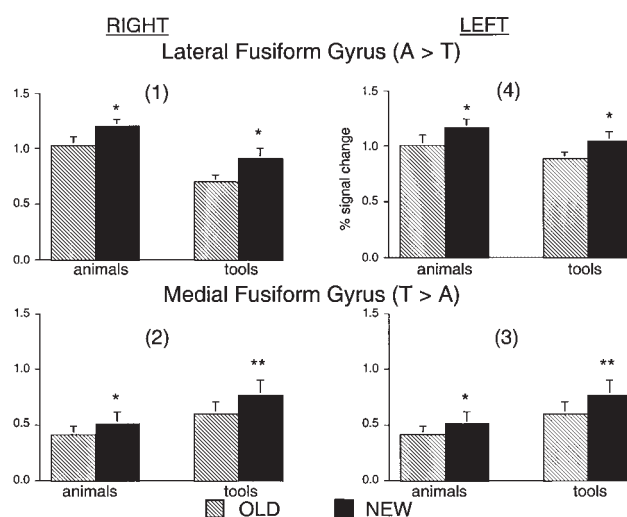
Figure 2. Mean amplitude of the fMRI signal in the regions of the fusiform gyrus depicted in Figure 1. The data are averaged across all repetitions of task blocks in each subject and across all subjects. Error bars indicate standard errors of the mean. Note the decrease in the fMRI signal associated with naming old pictures of animals and tools in both the lateral and medial regions of the fusiform gyrus, bilaterally ($^*P \leq 0.05$, $^{**}P \leq 0.01$).

studied 4 days earlier (old) produced significantly reduced responses relative to naming new pictures of these objects in all of these regions (Table 1 and Fig. 2). Thus, analysis of the data from the occipital and ventral temporal cortices yielded sig-

nificant main effects of category type (animal or tool) and experience (old or new), but no category × experience inter-actions.

In contrast, category × experience interactions were found in other regions of the brain. The comparison of naming animals versus naming tools revealed greater activity for animals in the right posterior STS and greater activity for tools in the left middle temporal gyrus, left ventral premotor cortex and left posterior parietal cortex, centered in the intraparietal sulcus (Fig. 3). There was a significant category × experience interaction in each of these regions, as prior experience only modulated activity for the category that showed a maximal response. For example, experience only modulated responses to pictures of animals in the right posterior STS. Naming new and old pictures of tools failed to produce activity in this region above the scrambled object baseline (Fig. 4). Experience only modulated responses to pictures of tools in the left middle temporal gyrus, left ventral premotor cortex and left posterior parietal cortex. Even though naming animals produced a significant response above the baseline in these areas there was no difference (either reduced or enhanced) between the responses associated with naming new and old pictures of animals (Fig. 4).

Still other regions showed a main effect of experience, but no effect of category or an interaction between category and experience. Relative to naming new pictures, naming old pic-tures elicited decreased activity bilaterally in the middle frontal cortex (BA 9 and 46), left inferior frontal cortex (BA 44 and45) and right anterior cingulate gyrus (Table 2). In contrast to these reductions, enhanced activity associated with naming old relative to new pictures was found in bilateral regions of the
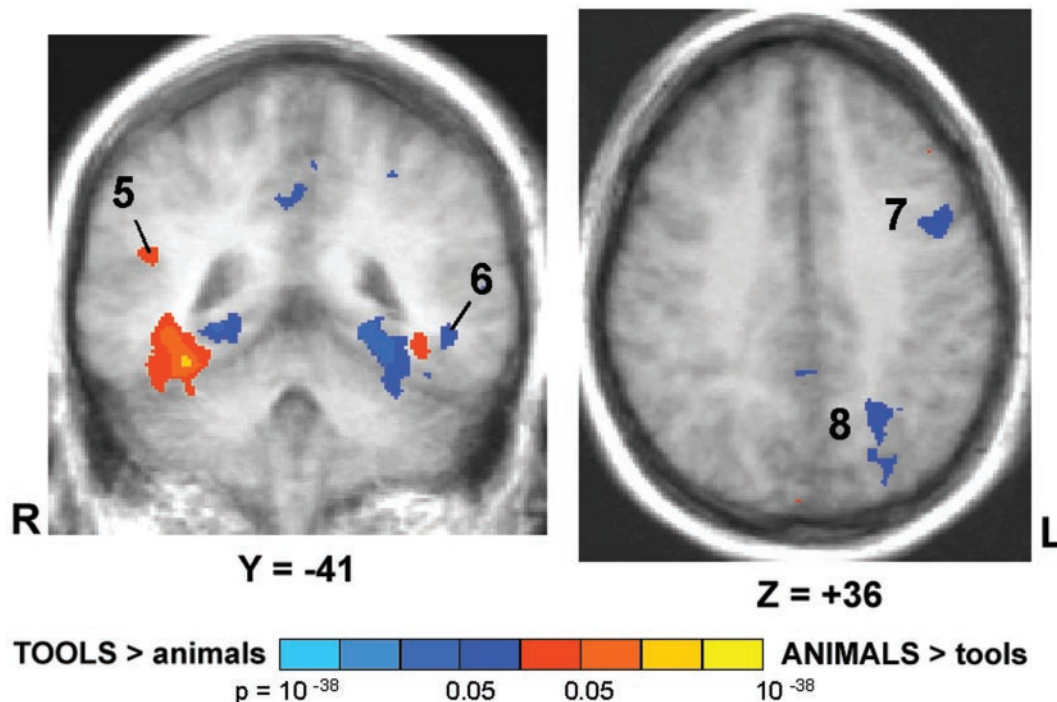
Figure 3. fMRI responses in the lateral temporal, left premotor and left parietal cortices during animal and tool naming. The averaged significance maps are overlaid on an averaged anatomical image from seven subjects. The maps, which are illustrated in coronal (y = −41) and axial (z = 36) sections, show the locations of the regions in the lateral temporal, left premotor and left parietal cortices that responded differentially to naming pictures of animals and tools. Within the lateral temporal cortex, the right superior temporal sulcus (5) responded maximally to naming animal pictures while the left middle temporal gyrus (6) responded maximally to naming tool pictures. In addition, regions within the left ventral premotor cortex (7) and left posterior parietal cortex (8) also responded maximally to naming tools.
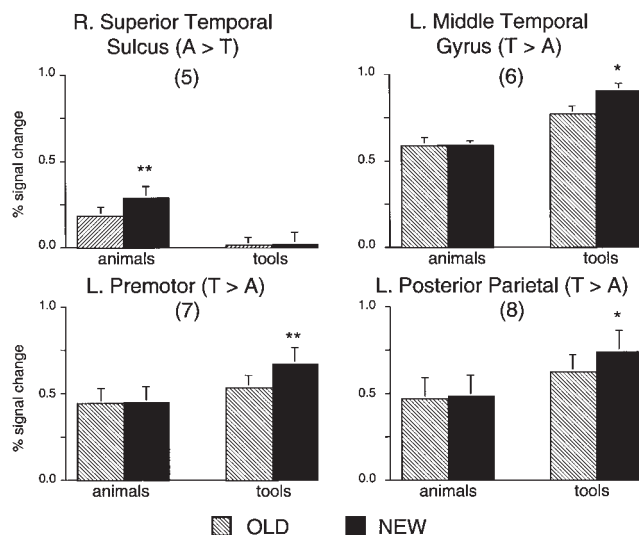
Figure 4. Mean amplitude of the fMRI signal in the regions depicted in Figure 3. A decrease in the fMRI signal in the right superior temporal sulcus (5) was only associated with naming old pictures of animals; pictures of tools did not elicit a response above the scrambled object baseline. Pictures of animals elicited a response above baseline in the left middle temporal gyrus (6) and premotor (7) and posterior parietal (8) cortices. Nevertheless, the decrease in the fMRI signal was only associated with naming old pictures of tools ($^*P \leq 0.05$, $^{**}P \leq 0.01$).

prefrontal cortex, anterior insula, precuneus, left hippocampus, left cingulate gyrus and right parahippocampal gyrus (Table 2 and Fig. 5).

Discussion

There were several main findings. First, silently naming pictures of animals and tools activated distinct, distributed cortical networks, replicating previous findings [reviews can be found elsewhere (Martin, 2001; Martin and Chao, 2001)]. Second, experience modulated (i.e. reduced) the activity in these category-responsive regions. The experience-dependent reductions were found for both object categories in some regions, but were limited to the category that elicited the maximum response in other regions. Third, activity was elicited by covert object naming in several brain regions that did not show a bias towards either category. Some of these non-category-biased regions showed reduced activity for old (familiar) relative to new (novel) stimuli while others showed enhanced activity for familiar relative to novel objects.

Modulation of Category-related Activity

Naming pictures of animals elicited widespread activity relative to naming tools in the ventral occipito-temporal cortex, with peak activations bilaterally in the calcarine cortex, middle occipital gyrus and lateral region of the fusiform gyrus. In contrast, relative to naming animals, naming pictures of tools elicited peak activity bilaterally in the more medial region of the fusiform gyrus. In the lateral temporal cortex, activity was strongest in the right STS for naming animals and in the left middle temporal gyrus for naming tools. Tool naming also resulted in stronger activity in the inferior region of the left intraparietal sulcus and left ventral premotor cortex than did animal naming.

As expected, prior exposure to a subset of the stimuli modulated activity in these regions. Moreover, the experience-dependent changes always consisted of a reduced response to

Table 2
Non-category-biased regions that showed experience-related changes in activity

Region	Learning effect	Talairach coordinates (x,y,z)		
Frontal				
L inferior frontal gyrus	N > O**	−38	14	12
	N > O*	−45	30	16
L middle frontal gyrus	N > O*	−39	23	28
R middle frontal gyrus	N > O*	42	26	26
R anterior cingulate gyrus	N > O*	3	20	36
Frontal				
L middle frontal gyrus	O > N*	−29	45	3
R orbital frontal	O > N*	14	48	−10
L cingulate gyrus	O > N*	−9	43	11
L insula	O > N*	−32	9	7
R insula	O > N*	36	1	11
Parietal				
L precuneus	O > N*	−8	−65	31
R precuneus	O > N**	5	−52	36
Medial temporal				
L hippocampus	O > N**	−28	−30	−3
R parahippocampal gyrus	O > N**	24	−35	−14

Center-of-mass coordinates from group-averaged statistical maps (*n* = 7) are reported in normalized stereotaxic space (Talairach and Tournoux, 1988). Z-scores > 4.50 for all regions.

R, right; L, left; O, old; N, new.

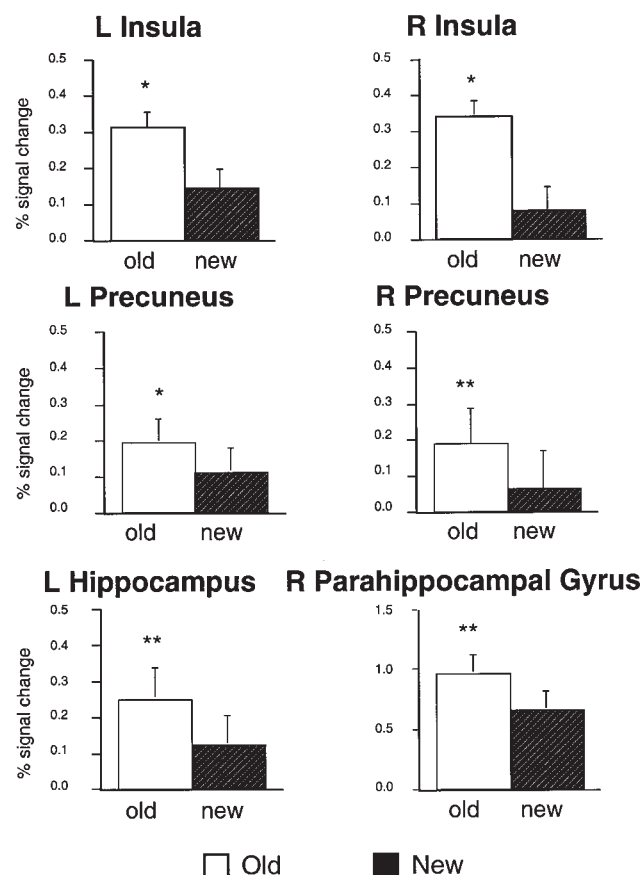Significance levels based on random effects ANOVA of the time-series data: *$P \leq 0.05$; **$P \leq 0.01$.

Figure 5. Mean amplitude of the fMRI signal in non-category-biased regions that showed learning-related increases in activity. Note that the fMRI signal is significantly increased for naming old as compared to new objects. (*$P \leq 0.05$; **$P \leq 0.01$.)

previously studied pictures relative to new pictures. These changes were widespread in the ventral occipito-temporal cortex, affecting the peak response (i.e. animals in the lateral fusiform gyrus and tools in the medial fusiform gyrus) as well as the smaller response associated with the other object category in each region (e.g. within the region of the lateral fusiform gyrus that responded maximally to animals, experience also reduced the response associated with naming pictures of tools).

To the extent that repetition-related reductions in the fMRI signal index changes in object-specific neural representations (Grill-Spector *et al.*, 1999) [reviews can be found elsewhere (Schacter and Buckner, 1998; Wiggs and Martin, 1998)] these results suggest that the representations of animals and tools are not restricted to the discrete areas that show a maximal fMRI response to each object category, but rather are distributed over a larger expanse of the ventral occipito-temporal cortex. This distributed view of object representation is consistent with recent electrophysiological recording studies of the ventral temporal cortex in humans (Kreiman *et al.*, 2000) and monkeys (Tsunoda *et al.*, 2001) and correlational analyses of the pattern of fMRI activity associated with viewing multiple-object categories (Haxby *et al.*, 2001).

The organizational principle of this region (e.g. why animal stimuli evoke a larger response in the lateral region of the fusiform gyrus and tool stimuli evoke a larger response in the more medial region) remains to be determined [although one possible scheme has been noted elsewhere (Levy *et al.*, 2001)]. The nature of the information stored in this area also remains to be specified. However, the location of these activations in the ventral object-processing stream suggests that a likely candidate is the features of object form shared by members of an object category (Haxby *et al.*, 2000; Martin *et al.*, 2000) [there is direct evidence of this possibility in the monkey cortex (Tsunoda *et al.*, 2001)].

Alternatively, rather than learning-related changes in object representation, experience-related reductions in the ventral occipito-temporal cortex may indicate a more general, non-specific change in processing, perhaps associated with reduced attention to blocks of familiar objects relative to blocks

of novel objects. However, two pieces of evidence argue against this view. First, in some brain regions, experience-related reductions were only observed for the object category that produced the maximal response in that region. Second, as will be discussed later, in still other regions, experience resulted in enhanced rather than reduced activity.

In contrast to the findings in the ventral occipito-temporal cortex, experience-dependent reductions in the lateral temporal cortex were limited to the object category that elicited the maximal response. Thus, a region in the right posterior STS, which was defined by a stronger response to animals than tools, showed reduced activity for naming familiar versus novel animal pictures. There were, however, no differences for naming familiar versus novel tool pictures, neither of which elicited activity above that for the scrambled object baseline in this region. Similarly, a region of the left posterior middle temporal gyrus, defined by a stronger response to tools than animals, showed reduced activity for naming familiar versus novel tool pictures, but no differences for naming familiar versus novel animal pictures. Even though the animal pictures elicited activity that exceeded that for the scrambled object baseline, this response was not affected by prior experience with the stimuli. These findings suggest that the information represented in the STS and middle temporal gyrus is relatively specific to each of these object categories. Again, the organizational principles and the nature of the information stored in these regions remain to be determined. However, the proximity of these activations to the brain area responsive to motion perception (i.e. MT) and the evidence reviewed earlier linking the

STS to biological motion and left middle temporal gyrus to non-biological motion suggest that these regions store information about object motion [recent reviews can be found elsewhere (Martin, 2001; Martin and Chao, 2001)]. Consistent with this proposal, it has recently been shown that the STS responds more to moving than to static images of human bodies and that the middle temporal gyrus responds more to moving than static images of tools, whereas activity in the ventral temporal cortex is not enhanced by motion (Beauchamp *et al.*, 2001).

A similar pattern of findings was found in the left intraparietal sulcus and left ventral premotor cortex. Both regions responded more to naming pictures of tools than animals, as we have previously reported (Chao and Martin, 2000), and both showed reduced activity for familiar relative to novel pictures of tools, but not for animals. Although naming animals produced a significant response relative to the baseline condition in these regions, the response was not modulated by experience. These findings suggest that category-related activity in these regions reflects the retrieval of stored information about features associated with tools but not animals (e.g. information about the patterns of motor movements associated with object use).

Taken together, these results are consistent with the idea that category-related activations represent the retrieval of information about features and attributes shared by members of a category, with features of form represented in a distributed fashion in the ventral occipito-temporal cortex, features of motion in the lateral temporal cortex and motor schemes associated with object manipulation in the intraparietal and premotor cortices.

Experience-dependent Modulation of Activity in Other Cortical Regions

Experience also modulated activity in several regions of the brain that did not show category-related differences. Regions in the middle frontal cortex, bilaterally, left inferior frontal cortex and right anterior cingulate showed decreased activity when subjects named familiar relative to novel pictures of animals and tools. Previous studies have reported decreased activity in similar regions of the left frontal cortex with item repetition (Demb *et al.*, 1995; Thompson-Schill *et al.*, 1997; Buckner *et al.*, 1998; Ranganath *et al.*, 2000; Wagner *et al.*, 2000) and several investigators have suggested that this region may be involved with retrieving and selecting information from semantic memory (Gabrieli *et al.*, 1998; Poldrack *et al.*, 1999; Thompson-Schill *et al.*, 1999; Wagner *et al.*, 2000). Thus, the current experience-related reduction in this area may be indicative of more efficient access to semantic information (e.g. the object's name) when that information has been recently retrieved.

In contrast to repetition-related decreases in activity, other non-category-biased regions showed enhanced activity for naming old relative to new pictures, including bilateral regions in the precuneus and prefrontal cortex, left hippocampus and right parahippocampal gyrus. These enhanced responses were not anticipated and, thus, caution must be exercised in interpreting their significance. However, it is noteworthy that all of these areas have previously been associated with retrieving information from episodic memory (Shallice *et al.*, 1994; Cabaza and Nyberg, 1997; La Bar *et al.*, 1999; McDermott *et al.*, 1999; Seger *et al.*, 2000). Although the current task (object naming) did not require subjects to explicitly recall previously studied items, this result suggests that at least part of the episodic memory system may be automatically engaged whenever familiar stimuli are encountered, regardless of whether subjects are required to recall or recognize the material presented explicitly [similar findings have been reported earlier (Koutstaal *et al.*, 2001)].

Finally, experience-dependent changes in two adjacent regions, the left inferior frontal gyrus and the anterior insula, deserve special mention. These areas showed opposite patterns of modulation: naming familiar relative to novel pictures resulted in reduced activity in the left inferior frontal gyrus and enhanced activity in the anterior insula. Similar patterns of experience-related changes have previously been reported in these regions (Raichle *et al.*, 1994; Van Turennout *et al.*, 2000). Moreover, it has been proposed that these opposing patterns of change reflect the transition from a more effortful mode of task performance with novel items to a more automatic mode of task performance with well-rehearsed items (Raichle *et al.*, 1994). The present findings are consistent with this possibility.

In summary, repeated exposure to and encoding of a relatively large number of items (360 pictures) 4 days prior to scanning resulted in relatively long-lasting changes in neural activity. These changes consisted of category-related reductions in neural activity that were widespread in the ventral occipito-temporal cortex and category-specific in the lateral temporal, inferior parietal and ventral premotor areas. Reduced activity was also observed in prefrontal regions associated with the retrieval of information from semantic memory. In contrast, enhanced activity to familiar stimuli was found in a network of regions associated with retrieval from episodic memory. Although, much work is needed in order to understand the implication of experience-dependent changes in neural activity, these results suggest that fMRI can be a useful tool for investigating learning-related cortical plasticity in the human brain.

Notes

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